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TICKS AS VECTORS OF ANIMAL DISEASES*

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OUTLINE

Kinds of ticks.
Tick habits and hosts.
Ticks and transmission of disease agents.
1. Methods of transfer.
2. Kinds of tick-borne pathogens.
3. Kinds of diseases and hosts affected.
4. Remarkable facts in tick-transmitted disease.
Other tick-caused conditions of animals. Effects of pathogens on ticks themselves.
Summary.

Ticks of various species are among the most important of the pests of animals, not only because of their direct effects as parasites, but also as a result of maladies they carry. Moreover, they are predisposing agents for attacks by important secondary invaders, such as foot-rot and screw-worm flies.

Information in the field of tick-borne maladies of animals is so rapidly expanding, and so scattered in the literatures of various countries that it is impossible in a program paper to attempt more than the briefest review. It will be evident from the subsequent discussion and tables that much of our progress has evolved about the attack on problems of disease transmissible to domestic animals and man. On the other hand, relatively little is known of tick-borne diseases that are strictly confined to the wild fauna, although this field is presumably also an extensive one.

Brief remarks on ticks themselves and their habits are needed to preface discussion of the diseases they carry among animals.

KINDS OF TICKS

There now are well over 400 known species of ticks, ranging in from 17 to some 30 genera, depending upon the authority consulted. They are grouped under two families, the Argasidae or "soft-bodied" ticks and the Ixodidae or "hard-backs." These popular terms are relative, referring to the absence or presence, respectively, of a hard, non-elastic, dorsal shield, complete in the male, incomplete in the female. In the ixodids the mouth-parts are terminal (prognathus), in the argasids, usually sub-terminal (hypognathus). Only a few minor genera containing obscure species do not have as yet some members incriminated in the transmission of some animal disease.

Ticks belong in the class Arachnida and are related to insects and their allies in having jointed appendages and external skeletal structures, but the mature forms differ from true insects in having eight legs and bodies undifferentiated into special regions.

TICK HABITS AND HOSTS

Unlike their closest relatives, the mites, only a small proportion of which are parasitic on animals, all ticks, so far as known, require vertebrate blood as food. Certain ticks show a wide host adaptability, while others are extremely restricted both as to the hosts and even the anatomical locations which they infest.

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Again, host relationships may vary with the stage of the tick concerned or with its geographic occurrence. Obviously the more cosmopolitan the distribution and the less restricted the host habits of a species, the greater its potentialities as a carrier of animal disease.

Mammals are most subject to tick attacks, but birds, particularly ground-frequenting species like the meadow-lark, and even reptiles and amphibians are utilized as hosts by certain species. Fish constitute the only group of vertebrates on which they are not at least occasionally encountered.

Geographically, ticks are distributed over all parts of the globe where hosts are available except the extreme frigid zones, but they reach their greatest specific diversification in tropical and subtropical climates.

The argasids are, for the most part, intermittent and relatively rapid feeders like some blood-sucking insects, while the ixodids usually remain attached to the host for some days or even weeks depending on the stage involved and other factors. However, even some argasids require long periods; for example, the nymphs of the spinose ear tick may remain on the host upwards of seven months. Some ixodids, on the other hand, become satiated in a very short time, such as the immature stages of *Haemaphysalis inermis* which have been observed to complete engorgement in as little as one to one and a half hours.

The number of instars of the argasids, even in a given species, is somewhat variable, there being from three to seven or even more molts, depending on the species and feeding conditions, while the ixodids molt only twice in passing through the larval and nymphal stages to the adult.

The unusual fecundity and longevity of many species of ticks also have important bearings on their rôle as vectors of disease. Argasids in particular are noted for their ability to survive without food for several years, while we have observed the Rocky Mountain wood tick, an ixodid, to persist unfed through the second and even into the third seasons under outside conditions. Many species produce an enormus quantity of eggs, five to ten thousand being not unusual; Bishopp and Hixon have reported the extreme of 18,497 eggs for one female of *Amblyomma maculatum*.

TICKS AND TRANSMISSION OF DISEASE AGENTS

The pioneer work of Smith and Kilbourne (1897) on tick-borne cattle fever of the southern United States was instrumental in focusing attention on the possibilities of arthropod transfer of the agents of disease. Subsequent study has revealed a wider variety of organisms transmitted by ticks than perhaps by any other one superfamily of arthropods. , These disease agents are usually transferred by tick bite, but in some instances also by coxal fluid or tick excrement. Tissues crushed on the skin are sometimes responsible for infection in man and presumably the same would hold true in animals.

Many infections are readily transmitted by all stages of ticks, while transfer of others may be restricted to a particular stage depending on factors of host susceptibility or variations in feeding habits of the ticks concerned. Except in the case of tick paralysis, both sexes are equally capable of transmitting disease.

No ticks are known to be restricted to parasitism of human hosts alone (certain argasids customarily frequent domestic habitations but will and do bite many types of animals, given the opportunity). For this reason, one may suspect any tick-carried pathogen of man as potentially involving lower vertebrate relationships even though recognized at present only as a human infection, e. g., tick bite fever of South Africa. There are many references in the literature to so-called "reservoirs" of such disease agents in nature. However, information as yet is too meagre to permit significant discussion of the controversial questions of the animal or tick origin of disease agents, or as to whether ticks or animals are the more important in perpetuation of such pathogens.

If space permitted, an enumeration of the specialized fields of science and industry that have contributed to our knowledge of the various phases of tick-carried diseases would emphasize the extensive ramifications of the subject.

1. METHODS OF TRANSFER

The following outline of methods of disease dissemination by arthropods among animals was adapted from several sources in connection with a discussion of flies as disease carriers (Philip, 1937) and serves as a basis for analysis of the ways in which ticks can act as agents in transmission of incitants of disease:

I. Mechanical transmission (the disease agent is merely transferred)
Simple carriers—as *Dermatobia cyaneiventris* by *Amblyomma cajennense*.
Direct inoculators—as surra and Chagas' disease by certain species of *Ornithodoros* (experimental).

II. Developmental transmission (the parasites grow or multiply during residence in the vector)
Incidental hosts (in which the pathogen multiplies, but the tick is not essential for perpetuation of the disease agent)—as tularaemia in several ixodid species.
Essential hosts (the tick is necessary in disease cycle)
For simple proliferation of disease agent—probably the tick-borne filtrable viruses analagous to yellow fever in the mosquito.
For simple development (i. e., without increase in numbers)—as possibly certain filariad worms by *Rhipicephalus sanguineus*.
For cyclic development—cattle fever and other tick-borne sporozoans by many ixodid species; spirochaetoses by argasids.

The last category is by far the most important and includes the big majority of the tick-borne pathogens.

Sharp lines are difficult to draw in such an outline. For example, while simple proliferation of *Bacterium tularense* occurs in the tick, it is still not an essential host for transfer of infection. And again, transfer of relapsing fever organisms (in certain instances) occurs through the bite wound or an abrasion in the skin of the host contaminated by the excretions of the coxal glands of feeding argasids. While this is in a sense mechanical, yet the spirochaetes are considered to have undergone proliferation in the ticks. Diseases of unknown aetiology, such as tick paralysis, possibly due to a toxin, cannot be classified satisfactorily at present. Furthermore, information is still too meagre for many of the known tick-borne maladies to be susceptible of satisfactory allocation in the above outline, except perhaps by analogy, e. g., rickettsioses and ultrascopic viruses.

Table I. KINDS OF PATHOGENS NATURALLY OR EXPERIMENTALLY CARRIED BY VARIOUS TICKS.

A. SPIROCHAETES—*Treponema duttoni* and varieties (or related species?); *T. anserina; T. theileri.*

B. FLAGELLATES—*Trypanosoma cruzi, T. evansi, T. christophersi (hyalommae).*

C. SPOROZOANS—*Babesia bigemina, B. bovis, B. motasi, B. ovis, B. trautmanni, B. leporis, B. canis, B. caballi, B. (Nicollia) quadrigemina, B. (Rossiella) rossi, B. (Piroplasma) gibsoni, B. (Rangelia) vitalii; Babesiella argentina; Theileria parva; T. stordyi, T. mutans, T. annulata (dispar); Eperythrozoon wenyoni; Nuttallia equi, N. minor; Anaplasma marginale* and var. *centrale, A. ovis; Hepatozoon (Haemagregarina) canis; Francaiella colchica, F. occidentalis, F. caucasica; Aegyptianella pullorum.*

D. RICKETTSIAS—*Dermacentroxenus rickettsi, Rickettsia ruminantium, R. canis, R. bovis, R. ovina, R.* sp. of "tick-bite fever."

E. BACTERIA—*Bacterium (Pasturella) tularense; Bacillus pestis* (?).

F. ULTRASCOPIC (FILTRABLE) VIRUSES—Nairobi sheep disease, louping ill, ovine "tick-borne fever", equine encephalomyelitis, rabbit papilloma (Shope virus), foot and mouth disease (?).

2. KINDS OF TICK-BORNE PATHOGENS

The incitants of animal disease conveyed naturally or experimentally by ticks represent six groups of disease agents, namely, the spirochaetes with three species and many strains (considered by some specialists rather as separate species), the flagellates with two or possibly three species, the sporozoans or piroplasms with twenty-seven species (there is disagreement among authorities in classification of these also), the rickettsias with six species, the bacteria with one and possibly a second species, and five ultrascopic or filtrable viruses. The species are listed in Table I. This list will undoubtedly be rapidly augmented as investigations continue.

Ticks have been accused or suspected of carrying a number of other diseases and are involved in certain additional derangements of animals as discussed hereafter. In the case of a few of the above infections, ticks are not the important or only agents of transmission.

3. KINDS OF DISEASES AND HOSTS AFFECTED

Tables are appended enumerating the various maladies, hosts, geographic occurrence, and associated ticks. The list of infections of domestic stock alone is a formidable one; many are of economic consequence in various parts of the world. It would be impossible here to more than briefly mention certain of the outstanding animal diseases carried by, or experimentally transferred by ticks.

In many instances, a particular pathogen may be capable of experimental transfer by several tick species, but in a given area, often only one vector may have the right host habits to be actually concerned. This is of real consequence in relation to control activities for certain of these diseases which are more important economically. For example, cattle fever or red-water can be transmitted by eight species of *Boophilus* and *Rhipicephalus*, but only one, *Boophilus annulatus*, is concerned in most of the southern United States, thus simplifying control measures because of restriction of the parasite in both the animal and tick hosts. Consider, on the other hand, the picture in tularaemia. This is a disease, widely distributed in the Northern Hemisphere, to which a large variety of vertebrates is subject, chiefly rodents, but larger mammals and birds may be affected as well. In North America alone, three species of *Dermacentor*, two of *Haemaphysalis* and one of *Ixodes* have been discovered naturally infected, while strong epidemiological evidence incriminates another, *Amblyomma americanum*. Experimentally, all North American tick species tried have been found capable of harboring the incitant, while most ixodids readily transfer it by bite. In our experiments little difficulty has been encountered in obtaining transovarial passage of *Bacterium tularense* in surviving ticks, but Russian workers report complete failure to carry these organisms into the second generation of two Siberian species of ticks.

In the case of certain diseases, ticks have been suspected as possible vectors, but observational and experimental evidence is as yet too meagre to consider them of more than doubtful significance. Among these may be included plague, verruga peruana, kala-azar, leishmaniasis, all human infections with other vector and animal implications.

Though reported experimentally, tick transmission of the filtrable viruses of equine encephalomyelitis, foot and mouth disease, and rabbit (Shope) papilloma also needs further study, while the observations of Aragao on tick-transmission of yellow-fever have not been confirmed. Tick implication in the first disease, however, would appear to be chiefly of academic interest since the epizootiology in the western United States, at least, does not conform to tick incidence on horses. The suggested possibility that ticks transmit piroplasmoses, e. g., *Karyolysus lacertarum* of snakes and lizards, also requires further study.

In addition, they have been accused, but not proved, as carriers of six species of filariid worms (*Dirofilaria imitis, Filaria mitchelli, F. martis, Dipetalonema perstands, D. grassi* and *D. reconditum*) as well as certain of pyogenic bacteria and vegetable parasites (e. g. *Histoplasma farcinimosum*, causing epizootic lymphangitis in certain animals).

4. REMARKABLE FACTS IN TICK-TRANSMITTED DISEASE.

Some unusual observations that have resulted from various studies warrant special mention. Among the most interesting are those of Rozenbusch and Gonzalez in experiments with *Boophilus microplus* in the transmission of piroplasmosis and anaplasmosis of cattle in the Argentine in which they found minimum effective temperatures for transfer of the former to be 29° C. and for the latter 34° C. This is suggested as explaining certain peculiarities in the epizootiology of these diseases.

Contrary to the characteristics of most sporozoans in ticks, African East Coast fever of cattle has been shown not only *not* to be passed through the egg, but in three host ticks (*Rhipicephalus appendiculatus, R. simis* and *R. capensis*) the infection is purged from the tick in the next stage after becoming infected, i. e., a larva acquires and retains the organisms into the nymphal stage but does not carry them into the adult stage unless reinfected whether or not the nymph feeds on a susceptible or an immune animal.

Perhaps more remarkable is the reported failure of the organism of African heartwater of cattle to be carried through the eggs into the succeeding generation of ticks. Other tick-carried rickettsias, so far as studied, show hereditary passage from one generation to the next.

Among the filtrable viruses, Nairobi sheep disease is reported to pass transovarially, but not from stage to stage for more than one molt (unless reinfection again takes place), whereas the viruses of louping ill and tick-borne fever of sheep persist through the three active stages but do not carry through the eggs. Syverton and Berry report survival of the virus of equine encephalomyelitis through all stages of *D. andersoni* including the egg, but we have been unable so far to confirm this with our strains of virus. The Shope papilloma of wild rabbits has, in one instance only, been mechanically transferred by nymphs of *D. andersoni* as reported by Larson, Schillinger and Green.

The three-host tick, *Rhipicephalus bursa,* is one of the ticks carrying red-water (Texas fever) in North Africa and passes the infection through all stages including the egg, but it has been reported to transmit the disease to cattle only as adults and not as larvae or nymphs. Biliary fever of dogs in Africa shows a similar relationship with *Haemaphysalis leachi.* In the case of another blood parasite of dogs in India (*Haemagregarina canis*), although transferred in *Rhipicephalus sanguineus* through the eggs and larvae, this tick is not infectious until the nymphal and adult stages.

The rickettsiae of Rocky Mountain spotted fever pass into an inactive phase during winter residence in the tick host which requires a subsequent exposure to vertebrate blood or incubation to again become virulent for susceptible animals. Intersexual transfer of these organisms has been demonstrated, particularly when non-infected female ticks are fertilized by infected males.

Strains of relapsing fever organisms in different parts of the world have become adapted to certain species of argasid ticks so that in some instances only one, in other instances a restricted number of species, perhaps even without geographic relationship, can act as experimental vectors. For example *Ornithodoros savignyi* has been shown to transmit the strains *duttoni, hispanica* and *persica,* while *O. tholozani* will carry only the last; *O. turicata* is infectible with none of the above, but with two Western Hemisphere strains, *T. turicatae* and *T. venezuelensis.*

While argasids act as vectors of most of the animal and bird spirochaetes, *Treponema theileri* of large domestic animals in Africa is transmitted by the ixodid species, *B. decoloratus* and *R. evertsi.*

These are but a few of many remarkable and important facts that are the outgrowth of research on tick-transmitted disease of animals.

OTHER TICK-CAUSED CONDITIONS OF ANIMALS.

In addition to disease caused by specific tick-borne pathogens, other adverse effects on the animal hosts due to tick parasitism have been discussed by various authors under the following heads, and need not be elaborated here:

1. Worry and loss of flesh.
2. Removal of blood through excessive infestation.
   a. Often resulting in death from anemia.
   b. Or lowering resistance to intercurrent disease.
3. Production of wounds and abscesses providing portals for local or systematic secondary infection.
4. Introduction of toxins or secretions causing local or systemic reaction, such as suggested in the case of tick paralysis.
5. By acting as intermediaries for infestation by other parasites such as *Dermatobia cyaneiventris* or certain filarial worms.

Judged by the excellent criterion of economic losses in domestic animals in various regions, the first four effects of tick infestation can be of serious consequence: the last category is probably of little importance.

EFFECTS OF PATHOGENS ON TICKS THEMSELVES

Adaptation between the tick vectors and some of the pathogenic organisms has not progressed to the same extent in all cases, and in a few instances the ticks themselves are adversely affected. None of the many species of sporozoans or strains of spirochaetes have been reported as deleterious to the associated ticks. However, we have observed *Bacterium tularense,* in spite of its wide host affinities, to result in death or impairment of reproductive processes in many ticks completing engorgement just before the death of the animal host, i. e., when bacteremia is most intense. Zassuchin and Tichomirova have also reported a lethal effect on ticks of ingested *Bacillus pestis.* Brumpt also has reported the pathogenic effect of excessive numbers of *Trypanosoma christophersi* (*hyalommae*) in ticks.

SUMMARY

Ticks of various species are among the most important of the pests of animals of every continent, both as a result of infections they transmit and because of their direct and indirect parasitic effects on the health of their animal hosts. Disease producing agents in animals, naturally or experimentally tick-borne, include a remarkably wide variety of organisms grouped under spirochaetes, sporozoans, flagelletes, rickettsias, bacteria, and ultrascopic (filtrable) viruses.

Tick hosts include all classes of vertebrates except fish; their habitats, the entire non-aquatic globe except the extreme polar regions. These facts and their parasitic habit in both the immature and adult stages, often on different animals (both individuals and species), predispose to the transmission of disease. No species are known to be solely parasitic on man, and it is therefore likely that all tick-borne diseases of man have their source in nature, as has already been shown for some. Ticks may act either as essential hosts in the transfer of a given infection, or, less frequently, as incidental or mechanical transmitters. They have also been accused as intermediate hosts of certain parasitic worms. Examples are cited of some remarkable biological facts that have resulted from investigations of tick-borne animal diseases. In a few instances, apparently incomplete adaptation between the pathogens and associated ticks results in some adverse effect on the ticks themselves.

Table II. TICK-TRANSMITTED SPIROCHAETES OF RELAPSING FEVER

SPECIES OF SPIROCHAETE	ANIMAL HOST (other than man)	TICK HOST	LOCALITY
Treponema theileri (ovina, suilla, equina)	large domestic	*Boophilus decoloratus* *Rhipicephalus evertsi*	East and So. Africa West Australia
anserina	domestic fowls and certain birds	*Argas persicus*	Almost world wide
duttoni (rossi, kochi)	rats and mice	*Ornithodoros moubata* *O. savignyi*	Central Africa
(crocidurae)	small rodents	*O. erraticus*	West and No. Africa
a. *hispanica*	many wild animals, particularly rodents	*O. erraticus*	North Africa
(marocana, peliponesica)	rodents	*O. savignyi*	No. Africa and Mediterranean countries
(eratici, gondii, normandi)	rodents?	*O. erraticus* *O. normandi*	No. Africa and Mediterranean countries
b. *persica*	rodents and small, domestic animals	*O. verrucosus*	Asia Minor and Central Asia
(sogdianum, usbekistanicum)		*O. tholozani, (papillipes)*	
c. *venezuelensis (neotropicalis)*	certain monkeys, opossums, armadillos, etc.	*O. venezuelensis* *O. talaje*	Northern South and Central America
d. *turicatae*	small rodents	*O. turicata*	Central U. S. and California

TICK-BORNE DISEASES OF ANIMALS. I. NORTH AMERICA

NAME OF DISEASE	ANIMAL HOSTS	TICK SPECIES	METHOD OF TRANSMISSION (in or by ticks)
Spirochaetes Relapsing fever	rodents	*Ornithodoros turicata* *O. hermsi* *O. parkeri*	developmental and hereditary
	fowl	*Argas persicus*	developmental and hereditary
Sporozoans			
Texas fever	cattle	*Boophilus annulatus*	developmental and hereditary
Anaplasmosis	cattle	*Dermacentor occidentalis*	developmental and hereditary
		Dermacentor, 2 other spp.	experiments have failed to show more than stage to stage transmission
		Rhipicephalus sanguineus	
		Ixodes scapularis	
Canine babesiosis	dogs	*R. sanguineus*	developmental and hereditary
Babesia caballi *Nuttalia equi*	horses (Central America)	?	?

Rickettsias			
Rocky Mountain spotted fever	rodents	*Dermacentor*, 4 spp. *Haemaphysalis leporis-palustris* *Amblyomma*, 2 spp.	developmental and hereditary
Bacteria			
Tularaemia	rodents, sheep	*Dermacentor*, 3 spp. *Haemaphysalis*, 2 spp. *Amblyomma americanum* *Ixodes ricinus californicus*	proliferative and hereditary
Ultrascopic viruses			
Equine encephalomyelitis	horses	*D. andersoni*	stage to stage, hereditary (experimental)
Shope virus	rabbits	*H. leporis-palustris*	mechanical (one experiment only)
Unclassed disease			
Tick paralysis	sheep, cattle	*D. andersoni*	during feeding of ♀
Anemia	rabbits, sheep, moose and deer?	*D. andersoni*	during feeding

TICK-BORNE DISEASES OF ANIMALS. II. SOUTH AMERICA

NAME OF DISEASE	ANIMAL HOSTS	TICK SPECIES	METHOD OF TRANSMISSION
Spirochaetes			
Relapsing fever	a variety of domestic and wild animals	*Ornithodoros talaje* *O. venezuelensis*	developmental and hereditary
	fowl	*Argas persicus*	developmental and hereditary
	horse	*Boophilus microplus?*	?
Sporozoans			
Piroplasmosis ("tristeza")	cattle	*Boophilus calcaratus* *B. decoloratus* *B. microplus*	developmental and hereditary
Babesiellosis	cattle	*B. microplus*	developmental and hereditary
Anaplasmosis	cattle	*B. microplus?* *B. australis*	developmental and hereditary
Equine babesioses	horses	*B. microplus?*	developmental and hereditary
Canine babesioses ("nambiuvu")	dogs	*Rhipicephalus sanguineus*	developmental and hereditary
Rickettsias			
Brazilian spotted fever	probably dogs	*Amblyomma striatum* *A. cajennense*	developmental and hereditary
Ultrascopic virus			
Yellow fever	certain primates	*A. cajennense* *O. rostratus*	experimental by bite, unconfirmed
Flagellates			
Trypansomiasis (Chagas disease)	armadillo, opossum, possibly certain domestic animals	*A. cajennense* *R. sanguineus*	mechanical

TICK-BORNE DISEASES OF ANIMALS III. EUROPE

NAME OF DISEASE	ANIMAL HOSTS	TICK SPECIES	METHOD OF TRANSMISSION
Spirochaetes			
Relapsing fever	rodents	*Ornithodoros savignyi*	developmental and hereditary
	fowl	*Argas persicus*	developmental and hereditary
Sporozoans			
Splenetic (Texas fever)	cattle	*Boophilus calcaratus* *B. schulzei?* *Haemaphysalis punctata*	developmental and hereditary
Bovine babesioses	cattle	*Ixodes ricinus* *I. persulcatus* *Haemaphysalis punctata*	developmental and hereditary
Biliary fever	dogs	*Dermacentor marginatus* *I. ricinus* *Rhipicephalus sanguineus*	developmental and hereditary
Equine piroplasmoses a. *Babesia caballi*	horses	*D. marginatus* *B. bursa?* *H. aegyptium?* *R. sanguineus*	developmental and hereditary
b. *Nuttalia equi*		*R. bursa*	developmental and hereditary
c. *N. minor*		*D. niveus*	developmental and hereditary
Ovine piroplasmosis	sheep	*R. bursa*	developmental and hereditary
Rickettsias			
Boutonneuse fever	dogs	*R. sanguineus*	developmental and hereditary
Ovine rickettsiosis	sheep	*R. bursa*	developmental and hereditary
Bacteria			
Tularaemia	several rodents	not stated	
Ultrascopic viruses			
Louping ill	sheep	*I. ricinus*	Probaby proliferative; stage to stage, but not hereditary
Tick-borne fever	sheep	*I. ricinus*	
Unclassed diseases			
"Jaunisse mortelle"	dogs	*I. hexagonus*	?
"Jaunisse toxique"	dogs	*R. sanguineus*	?
Tick paralysis	sheep	*I. ricinus*	during feeding of female

TICK-BORNE DISEASES OF ANIMALS IV. AFRICA

NAME OF DISEASE	ANIMAL HOSTS	TICK SPECIES	METHOD OF TRANSMISSION
Spirochaetes			
Relapsing fever	large domestic	*Boophilus decoloratus*	developmental and hereditary
		B. annulatus	
		B. australis	
		Rhipicephalus evertsi	
	fowls	*Argus persicus*	developmental and hereditary
		Ornithodoros moubata	
	rodents	*O. moubata*	developmental and hereditary
		O. marocanus	
Sporozoans			
Red-water	cattle, sable antelope	*B. decoloratus*	developmental and hereditary
		R. appendiculutus	
		R. evertsi	
		R. bursa	
Biliary fever	dogs	*Haemaphysalis leachi*	by adults only, but developmental and hereditary
		R. sanguineus	developmental and hereditary
Biliary fever (babesiosis)	solipeds including zebra	*Hyalomma aegyptium*?	not known
		Boophilus spp.	
Biliary fever (nuttalliosis)	solipeds including zebra	*R. evertsi*	developmental, but hereditary not proved
East Coast fever	cattle	*Rhipicephalus*, 4 spp.	developmental, but not hereditary
		H. impressum	
Pseudocoast fever	cattle	*R. evertsi*	developmental, but not hereditary
		R. appendiculatus	
Transcaucasian fever	cattle	*H. mauritanicum*	developmental, but not hereditary
		H. impressum	
(Theileria stordyi)	gazelle	?	?
Fowl piroplasmosis	fowls	*Argas persicus*	probably developmental
Gallsickness (Anaplasmosis)	cattle and sheep	*B. decoloratus*	developmental and hereditary
		Rhipicephalus, 3 spp.	
		Ixodes ricinus	
Nicollia quadrigemina	rodents	?	?
Rossiella rossi	jackal	?	?
Rickettsias			
Heartwater	ruminants	*Amblyomma hebraeum*	developmental but not hereditary
		A. variegatum	
Kenya "tropical typhus"	dogs?	*R. sanguineus*	?
		R. pulchellus?	
Canine rickettsiosis	dogs	*R. sanguineus*	developmental and hereditary?
Ovine rickettsiosis	sheep	*R. bursa*	?
Tick-bite fever	dogs? rats?	*A. hebraeum*	developmental and hereditary, probably
		R. appendiculatus	
		B. decoloratus	
		H. aegyptium	
		H. leachi	
Ultrascopic virus			
Nairobi sheep disease	sheep	*R. appendiculatus*	Proliferative (?) and hereditary
		A. variegatum	Hereditary not proved
Unclassed disease			
Tick paralysis	sheep	*Ixodes pilosus*	During period of feeding of female
		I. rubicaudus	

TICK-BORNE DISEASES OF ANIMALS V. ASIA

NAME OF DISEASE	ANIMAL HOSTS	TICK SPECIES	METHOD OF TRANSMISSION
Spirochaetes			
Relapsing fever	rodents and small domestic animals	*Ornithodoros verrucosus*, *O. tholozani*, *O. lahorensis*	developmental and hereditary
	fowl	*Argas persicus*, *A. mianensis*	developmental and hereditary
Flagellates			
Indian surra	large domestic	*O. tholozani*, *O. lahorensis*	mechanical (experimental)
Sporozoans			
Splenetic (Texas fever)	cattle	*Boophilus shariffi*? *B. schulzei*	developmental and hereditary
Anaplasmosis	cattle	*Boophilus*, 3 spp.	developmental and hereditary
Theileriasis	cattle	*Hyalomma* 2 spp.	developmental but not hereditary
Eperythrozoiasis	cattle	*Hyalomma* sp.	?
Biliary fever	horses	*Dermacentor silvarum*	?
Biliary fever	dogs	*Rhipicephalis sanguineus*, *Haemaphysalis bispinosa*	developmental and hereditary
Canine malaria	dogs	*R. sanguineus*	stage to stage; hereditary?
Rickettsias			
Bovine rickettsiosis	cattle	*Hyalomma* sp. (undet.)	stage to stage; hereditary?
Indian tick-typhus	"some native mammal"	*R. sanguineus*, *R. haemaphysaloides*?	unknown
Bacteria			
Tularaemia	rodents	*Dermacentor silvarum*, *H. punctatum*	experimental, only stage to stage, hereditary negative so far

FOOD HABITS OF *PHYMATA PENNSYLVANICA AMERICANA* MELIN (HEMIP.)*

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In a general way, the ambushing habits and preying adaptations of Phymatidae are familiar to all entomologists. Yet, as shown by the bionomic summary for this family included by Readio (27) in his paper on the feeding methods and life history of *Phymata erosa fasciata* (Gray) at Lawrence, Kansas, only a handful of food records have appeared in the literature, and studies of the conditions surrounding the preying process in nature are lacking entirely. An opportunity to contribute toward such studies was found in the vicinity of Urbana-Champaign in the summer and fall of 1938, when *Phymata pennsylvanica americana* was present in good numbers. Observations in nature were made on 35 field trips between July 30 and October 21, exclusive of August 11 to September 1.

TABLE 1. INSECT PREY OF *PHYMATA*

Systematic Position of Prey Taken			Specimens	Inclusive
Genus	Species	Family	Captured	Dates
	Coleoptera			
Batyleoma	*suturale* (Say)	Cerambycidae	1	VII-30
Diabrotica	*duodecimpunctata* (Fab.)	Chrysomelidae	36	VII-5:X-17
Diabrotica	*longicornis* Say	Chrysomelidae	12	IX-7:X-11
Diabrotica	*vittata* (Fabr.)	Chrysomelidae	2	X-7:X-9
Mordellistina	*comata* (Lec.)	Mordellidae	3	IX-3:IX-8
Desmorus	*fulvus* Lec.	Curculionidae	1	IX-8
	Hymenoptera			
Atrometus	*clavipes* (Davis)	Ichneumonidae	2	IX-8:IX-14
Apanteles	*forbesi* Vier.?	Braconidae	2	X-5:X-8
Bassus	*annulipes* (Cr.)	Braconidae	1	IX-16
Chelonus	sp	Braconidae	2	IX-4:X-3
Bruchophagus	*gibbus* (Boh.)	Eurytomidae	1	X-5
Macrorileya	*acanthi Ashm.*	Eurytomidae	1	IX-5
Aprostocetus	sp.	Eulophidae	1	X-5
Psithyrus	*variabilis* Cress.	Bombidae	1	X-10
Apis	*mellifica* Linn.	Apidae	12	VIII-4:X-11
Halictus	*ligatus* Say.	Halictidae	2	VII-30:X-16
Halictus	*stultus* Cr.	Halictidae	1	X-5
Halictus	sp.	Halictidae	5	X-1:X-17
Augochlorella	*striata* (Prov.)	Halictidae	1	X-1
Sphecodes	sp.	Halictidae	1	X-5
Melissodes	*obliqua* Say	Eucerídae	1	VIII-6
Pseudopanurgus	*simulans* Sw. and Ckl.	Panurgidae	1	IX-27
Formica	*pallidefulva nitidiventris fuscata* Em.	Formicidae	1	X-7
	Lepidoptera			
Pieris	*rapae* L.	Pieridae	2	X-7:X-14
Colias	*eurytheme* Bdv.	Pieridae	7	VIII-9:X-15
Phyciodes	*tharos* (Dru.)	Nymphalidae	6	IX-29:X-17
Urbanus	*communis* (Grt.)	Hesperiidae	1	X-7
Atrytone	*ruricola* (Bdv.)	Hesperiidae	1	VII-31
Polites	*themistocles* (Latr.)	Hesperiidae	2	VIII-9
Polites	*peckius* (Kby.)	Hesperiidae	8	VIII-4:X-7
Heliothis	*obsoleta* (F.)	Noctuidae	1	IX-14

*Contribution number 208 of the entomological laboratories, University of Illinois. Grateful acknowledgments are made to the following for determinations: Mr. C. F. W. Muesebeck and his staff, U. S. National Museum, most prey insects; Professor C. L. Metcalf, my colleague, certain Syrphidae; J. Harwood Evans, Oshkosh High School, Oshkosh, Wisconsin, Phymatidae; Professor H. J. Fuller, James Hutchinson and W. E. Wilson, University of Illinois, ambush plants.

Agrotis	*venerabilis* Wlk.	Noctuidae	2	X-3
Feltia	*subgothica* (Haw.)	Noctuidae	10	IX-5:X-3
Scotogramma	*trifolii* (Rott.)	Noctuidae	2	IX-3:IX-7
Autographa	*precationis* (Gn)	Noctuidae	2	IX-3:X-10
Caenurgina	*crassiuscula* (Haw.)	Noctuidae	3	IX-2:IX-8
Plathypena	*scabra* (F.)	Noctuidae	1	IX-5
Scepsis	*fulvicollis* (Hbn.)	Syntomidae	2	VIII-10:X-15
Loxostege	*similalis* (Guen.)	Pyralidae	1	IX-3
	Diptera			
Aedes	*vexans* (Mg.) ♂	Culicidae	1	X-3
Eugnoriste	*occidentalis* Coq.	Mycetophilidae	10	IX-9:X-11
Sciara	*jucunda* Joh.	Mycetophilidae	1	IX-6
Sciara	spp.	Mycetophilidae	2	VIII-9:X-15
Dilophus	*breviceps* Lw.	Bibionidae	1	IX-4
Empis	*clausa* Coq.	Empididae	2	IX-6
Drapetis	sp.	Empididae	1	X-5
Saltella	*scutellaris parmensis* (Rond.)	Sepsidae	1	IX-7
Systoechus	*vulgaris* Lw.	Bombyliidae	4	VIII-4:IX-4
Hylemyia	spp.	Anthomyiidae	5	VIII-9:X-3
Pollenia	*rudis* (Fabr.)	Calliphoridae	12	VIII-3:X-27
Sarcophaga	*l'herminieri* Bd.	Sarcophagidae	4	VIII-9:X-5
Sarcophaga	*tenuiventris* V. d. W.	Sarcophagidae	3	VIII-9:X-11
Sarcophaga	near *pachyprocta* PK.	Sarcophagidae	1	X-3
Sarcophaga	*prohibita* Ald.	Sarcophagidae	1	VIII-9
Sarcophaga	*haemorrhoidalis* (Fall.)	Sarcophagidae	1	VIII-9
Sarcophaga	*reversa* Ald.	Sarcophagidae	2	VIII-10
Archytas	*apicifera* (Wlk.)	Tachinidae	1	VIII-3
Archytas	*basifulvus* (Wlk.)	Tachinidae	8	X-11:X-15
Plagiomima	*cognata* Ald.	Tachinidae	1	VIII-10
Cylindromyia	*argentea* (Tns.)	Tachinidae	1	X-10
Copecrypta	*nitens* (Wd.)	Tachinidae	2	X-15:X-17
Gymnosoma	*fuliginosa* Rd.	Tachinidae	2	X-15:X-17
Bonnetia	*compta* (Fall.)	Tachinidae	2	X-11:X-15
Gymnoclytia	*occidua* (Wlk.)	Tachinidae	1	X-17
Hyalomya	*calyptratae* (Coq.)	Tachinidae	2	IX-23:X-10
Chrysogaster	*nitida* Wied.	Syrphidae	1	VIII-4
Pipiza	sp.	Syrphidae	1	X-5
Eristalis	*tenax* L.	Syrphidae	2	VIII-3:X-17
Syritta	*pipiens* L.	Syrphidae	3	VIII-9:X-11
Melanostoma	*mellinum* L.	Syrphidae	2	IX-16
Allograpta	*obliqua* Say	Syrphidae	1	IX-27
Metasyrphus	*wiedmanni* (John.)	Syrphidae	1	IX-27
	Hemiptera			
Cosmopepla	*bimaculata* (Th.)	Pentatomidae	1	VIII-4
Lygus	*pratensis* (L.)	Miridae	13	IX-3:X-21
Plagiognathus	sp.	Miridae	1	VIII-9
Adelphocoris	*rapidus* (Say)	Miridae	3	IX-8:IX-16
Reuteroscopus	*ornatus* (Reut.)	Miridae	1	IX-10
Orius	*insidiosus* (Say)	Anthocoridae	3	IX-16:X-7
Ligyrocoris	*diffusus* (Uhl.)	Lygaeidae	1	IX-7
Nabis	sp. (large nymph)	Nabidae	1	IX-3
	Homoptera			
Phlepsius	sp.	Cicadellidae	1	IX-24

Summary of Tabulated Records. All the prey captured were insects, and with the exception of the damselbug nymph (Nabidae), all were adults and winged. Of the 25 orders forming the class Insects, only 6 were represented in the food table: these were Coleoptera, 6 species, 55 individuals; Hymenoptera, 17 species, 36 indviduals, Lepidoptera, 16, 51; Diptera, 33, 83; Hemiptera, 8, 24, and Homoptera, 1, 1. In addition to those tabulated, several species, including a tiny flea beetle (Halticini) were inadvertently lost in the field. Ten per cent of the prey individuals secured are Heterometabola and 90 per cent Holometabola.

General Features of Prey Chosen. First, the range in size is extreme. The smallest and weakest are the Mycetophilidae, *Sciara* and *Eugnoriste,* the anthocorid, *Orius insidiosus* and the mirid,*Plagiognathus* sp., which do not measure over 3 mm. long. Largest in size, and possibly as strong as any other species, are the several kinds of Noctuidae and the pierid butterfly, *Colias eurytheme,* with wing spreads of 34 and 54 mm., respectively. The most bulky prey caught was a male of the parasitic bumblebee, *Psithyrus variabilis,* but this instance is not normal since the bee was numb with cold and resistless when caught. Among the next larger victims were the drone fly, *Eristalis tenax,* tachinid flies of the genus *Archytas,* and the honey bee. But the majority of the catches measure between 5 and 10 mm. in length, notably the Chrysomelidae, Halictidae, Sarcophagidae, most Tachinidae and Syrphidae, and the Miridae.

Although several distinct types of mouth parts,—chewing, siphoning, sponging, piercing-sucking and lapping-sucking, are employed, all the insects secured as prey by *Phymata* have in common the one characteristic that they derive their food from some part of the flower, or possibly prey on some other insect there. Their plant food consists, as a whole, of pollen, nectar, petals, sepals, rays, and other parts, or probably sometimes sap, e. g., the Miridae. In coming to the flower to feed, these diverse mouth parts, and the antennae, the legs, in some cases the palpi and occasionally the wing margins, are brought within reach of the *Phymata,* so that the visitor becomes susceptible to capture.

Again, since the prey insects are almost invariably winged, their ability to fly readily enables them to visit many flowers of different kinds daily in their search for food, thus incidentally increasing the chances of being caught by the ambush bug.

However, *Phymata pennsylvanica* can not utilise all flying insects, regardless of size, that visit flowers to feed. Immune to attack were the tree cricket, *Oecanthus nigricornis,* the curculionid, *Rhynchites hirtus,* the meloid beetle, *Epicauta pennsylvanica,* the soldier beetle, *Chauliognathus pennsylvanicus,* males of *Bombus americanorum,* the vespid wasp, *Polistes annularis,* both males and females, the bombyliid fly, *Exoprosopa fasciata,* a small geometrid larva, and a yellowish caterpillar that seems to eat pollen in *Helianthus.* All of these were common to plentiful from time to time in one ambush plant or another. Their escape from attack can safely be attributed mostly to their superior size and strength or lack of convenient grasping points for the ambush bug. *Rhynchites* and *Epicauta* fed largely in the flowers of rosin weed, *Silphium integrifolium,* which *Phymata* rarely employed for ambush. Therefore, although this predator chooses prey from a large number of insects characterized by great variety in habit and structure, and may accordingly be described as opportunistic, its opportunism is considerably circumscribed.

Choice of Ambush Plants. On very warm days with little or no wind, ambush bug commonly flew about, and readily took to flight when disturbed. On such days, they also rested on the leaves or stems of flowering plants or on plants lacking flowers entirely. These observations indicate that flowers, i. e. ambush places, are found by trial and error, possibly guided by sight or odor, but sense reactions have not been investigated.

The duration of the stay in the flower is contingent on availability of prey and possibly the color agreement of bug and flower. The earlier published statements stated or implied that the Phymatidae choose flowers whose color harmonize with their own, and that, as a result, the ambush bug either escaped its enemies or had more success in the capture of prey. Early writers observed, what has been long verified, that the large open flower heads of Compositae possessing yellow flowerets and rays, and the spike-like yellow clusters of golden rod usually constitute the hiding quarters of the ambush bug. In the present

study, the Compositae most frequently inhabited were *Rudbeckia triloba* (thin-leaved coneflower), *Vernonia illinoisensis* (Illinois ironweed), *Bidens* sp. (beggartick), *Helianthus tuberosus* (Jerusalem artichoke), *Aster multiflorus* (many-flowered aster), and *Solidago* spp. (goldenrod). *H. tuberosus* and *Solidago* bloomed in profusion for several weeks while the adult ambush bug was at its numerical peak and probably harbored more than half of the ambush bugs observed in the whole season. Other Compositae utilised included *Eupatorium* (thoroughworts), *Lepachys pinnata* (yellow coneflower), *Erigeron annus* (white cap), *Cirsium altissimum* (tall thistle), and *Aster novae-angliae* (New England aster).

Outside the family Compositae, flowers more or less frequented were: *Apocynum cannabinum* (Indian hemp), Apocynaceae; *Asceepias incarnata* (swamp milkweed), Asclepidaceae; *Melilotus alba* (White sweet clover), Leguminosae; *Phycnanthemum flexuosum* (mountain mint) and *Monarda fistulosa* (wild bergamot), Labiatae; *Oenothera biennis* (common evening primrose), Onagraceae, and *Daucus carota* (wild carrot), Umbelliferae.

While most of the flowers harboring *Phymata* are large and predominantly yellow or brown, several noteworthy exceptions occur. In August, Indian hemp, ironweed and mountain mint formed the principal ambush plants, both in number of flowers and in the number of *Phymata* occupying them. The flower of Indian hemp is small, compact and pink, therefore not well suited for concealment; that of the ironweed, while just large enough to accomodate one *Phymata,* is usually purple or tinged with violet, and the flower cluster of mountain mint is entirely pale grayish green. Also the heads of thoroughwort, like the above, are not yellow and brown like *Phymata* and most of its ambush plants, but have purplish bracts and flesh-colored florets. It was common to see Phymatas balanced conspicuously on the small flowers of Indian hemp and even more often on the small unopened purplish flower buds of the ironweed. At the height of its bloom, a dense patch of the mint 15 feet square was inhabited by 55 *P. pennsylvanica* simultaneously. No concentration at all comparable to this was found even on heavy stands of goldenrod,—the most perfect ambush flower from the standpoint of concealing color and structure. These facts suggest that color agreement between flower and *Phymata* does not play the chief role in determining duration of stay in these instances.

Evidences obtained indicate quite conclusively, on the other hand, that such duration is influenced largely by the adequacy of the prey available in a given situation. Proof is afforded by the common to plentiful occurrence of *Phymata* on the flowers of Indian hemp, ironweed and mountain mint. Although not harmonious with the ambush bug in color, they nevertheless possess certain means of attracting an adequate supply of prey insects. Particularly noteworthy is the ironweed, whose small compact buds lack odor but yield a fluid attractive to many Diptera. Altogether, 36 insects, largely flies, with a few Lepidoptera, were taken from the ambush bugs on the buds and flowers of this plant.

The rosin weed and common evening primrose afford indirect evidence on this point. So far as favorable color is concerned, both should detain *Phymata* as long as they bloom, but this insect rarely occurred on either of them, even though both were common near or among fresh-blooming *Helianthus* and goldenrod. Moreover, neither of them attracted many potential prey insects, and none such were ever found in the grasp of the ambush bug on these plants. Primrose flowers remain closed all day, while those of rosin weed were rarely visited except by the immune beetles, *Rhynchites* and *Epicauta.*

Further evidence that availability of prey affects duration of stay in flowers is furnished by the very obvious migration of *Phymata.* These movements coincide with the succession, the coming and going, of the blooming periods of

different ambush plants. In August, mountain mint, Indian hemp and ironweed constituted the principal ambush plants; in September, goldenrod and *Helianthus tuberosus* dominated, and in October, when the *Phymata* tapered off numerically, *Bidens* and asters, especially *Aster multiflorus*, became the principal hiding places. So long as the flowers of any plant remained fresh in pollen and nectar and thereby attracted prey species, the ambush bugs persisted on them. Hereafter, they took wing to explore for new feeding areas. This was convincingly demonstrated on several patches of goldenrod, which, although not far apart, bloomed at somewhat different times. When only a half dozen fresh flower heads remained in an early blooming stand, among thousands that had already turned to the dull gold following the pollen stage, the ambush bugs gathered on the blooming few still visited by the *Diabrotica* species, *Archytas* and other insects. Almost daily checks showed as many as 6 to 12 ambush bugs consistently present on such small isolated plants as long as a week. As these flowers faded, the bugs gradually departed, and made their appearance on a nearby patch of goldenrod that developed flowers later and whose pollen again attracted good numbers of food insects.

Relative Prey–Attracting Value of Ambush Plants. While the flowers of 18 species of plants were used for ambush, only 11 of them harbored Phymatas in actual possession of prey. The unproductive 8 were white cap, New England aster, evening primrose, wild bergamot, thoroughwort, swamp milkweed, sweet clover and wild carrot. White cap and the aster bloom late when most ambush bugs have died or atmospheric temperatures are less favorable to their activities. Thoroughwort was observed irregularly, while the other 5 served but infrequently for ambush.

The eleven productive ambush plants were golden rod, mountain mint, ironweed, Indian hemp, yellow coneflower, rosin weed, Jerusalem artichoke, beggar tick, many-flowered aster and tall thistle. These exhibit pronounced differences in prey-attracting value, which are explicable in terms of (1) kind and amount of food afforded by the flowers to potential prey insects, (2) structure of the flowers affecting feeding by the insects, (3) food preferences and mouth parts of the insect visitors, and (4) seasonal differences in the blooming time of the ambush plants and in the occurrence of the prey species. These factors are reflected by the data in table 2, which includes figures for the eight most- captured prey species on the four dominant ambush plants, with reference to their major blooming times,–ironweed in August and *Aster multiflorus* in October, whereas goldenrods and artichoke occupied the intervening time and also overlapped the blooming periods of ironweed and aster.

TABLE 2. PREY CAPTURED ON DOMINANT AMBUSH PLANTS.

Ambush Plant	Apis mellifica	Eugnoriste occidentalis	Archytas basifulvus	Pollenia rudis	Diabrotica 12–punctata	Colias eurytheme	Feltia subgothica	Lygus pratensis
Illinois ironweed	1	0	0	12	1	1	0	0
Goldenrods	0	9	0	2	9	0	1	4
Jerusalem artichoke	2	0	0	1	17	2	5	6
Many-flowered aster	6	1	8	0	2	4	1	6

Capture of Prey. The remarkable modifications of the fore legs of Phymatidae for grasping are familiar to all entomologists. The short labium is thick at the base and tapers apically,–features that doubtlessly also facilitate the predatism of these bugs. The tapered apices of the maxillary stylets are expanded spatula-like and attenuated at the sides. The mandibular pair has no marginal teeth, such as occur in some predacious bugs, but its outer surface

is equipped with about 8 obliquely transverse parallel ridges that form a rasp.

When frequenting Compositae, *Phymata pennsylvanica* mostly stands in full view in an oblique posture on the lateral slope of the flower disk, with the raptorial legs only partly extended in readiness to seize prey. It also very commonly obscures itself among the more or less overlapping marginal rays of the flower head, poking its anterior end up between them with fore legs set for action. In golden rod, most of the body may be hidden among the flowers on the spike, and in thistle only the head and fore legs may remain in view as the insect stands almost vertically on end in the downy inflorescence. Commonly they also waited strictly on the outer or under sides of the heads, between two adjacent heads in contact, and at the base or on the upper surface of unopened flower buds, notably those of ironweed.

As the prospective prey insect moves over the ambush plant, it senses the parts of the flower with its palpi or antennae, treads on them with its feet, or introduces siphon, labella, lapping organ or jaws into them to take nectar, pollen, tissue or sap. Incidental to such activities, the visitor may bring one of these parts within reach of the raptorial legs of *Phymata* that waits quietly and never aggressively pursues the potential victim. At most, it orients itself so that it heads toward the approaching insect. Although several individuals were seen to seize prey, the movements of the fore legs were so quick and obscure that the eye could not follow them. But since the bug holds its grasping mechanism only in part extended while waiting prey, this device is obviously capable of further extension when some prey insect comes within grasping distance. An observed attempt on a *Systoechus vulgaris* failed, probably because the intended booty was slightly beyond grasping distance.

The part of the prospective prey by which *Phymata* takes hold varies considerably, but is presumably that appendage which extends free from the body and chances first to afford a holding point. By means of a reading glass used in the field, the tiniest insects, e. g. *Sciara* and *Eugnoriste* were seen to be invariably clamped bodily between the tibia and femur of one fore leg, whereas all other, or larger, prey species were grasped by some one extended appendage, the predator again employing but a single front leg in doing so. Thus, moths and butterflies were seized near the apex of the siphon extended in the act of feeding, Diptera were commonly caught by the labium while it was in use, while bees and beetles were more often seized by the antennae, presumably as they employed them in sensing the flower for food. However, there was no uniformity in the part seized in any order group. Altogether the original holding points were the antennae, mouth parts, excepting the mandibles of chewing insects, rarely the palpi and perhaps most often the forelegs.

The Feeding Process. When a *Phymata* was seen to capture a 12-spotted *Diabrotica* in *Helianthus,* the two were taken aside for close observation with the reading glass. The process, as described in this case, is known from supplementary instances to be essentially typical of other prey groups. As soon as the beetle was seized, it resisted vigorously but the predator calmly held it and at the same time probed its exoskeleton with the stylets. During the probing act, the stylets flickered rapidly back and forth at the end of the labium. In less than a minute these organs penetrated the body wall; before three minutes elasped the victim was obviously dead and its abdomen had become inflated to its maximum length and thickness, converting this body region into a sharp-tipped turgid cone. In all probability, this condition was effected by the injection of a salivary secretion.

During the meal taken in the following 70 minutes, the predator withdrew the stylets 17 times and, of course, reinserted them as often. The intervals between removal and insertion were devoted to manipulating its prey, probing

the skeleton for new entrance places, feeding, and perhaps injecting additional digestive fluid after some of the contents had been sucked out. In the process of manipulation, the beetle was turned into almost every conceivable position, placing all its parts,—from head to cauda, top to bottom, and even the legs, within reach of the stylets sooner or later. To accomplish this work, *Phymata* necessarily holds its dead prey continually in its raptorial legs, usually employing only one, but occasionaly both, e. g., one holding to an antenna, the other to a leg, proboscis or even a wing margin.

During the meal the dead beetle was released but rarely, and then only very briefly except near the completion of the meal. The stylets were introduced at many different places, but always at the points offering least resistance. Such were the mouth of the beetle, the points of articulation of the antennae, legs and wings with the body, the conjunctivae joining the body regions and their segments, and even the joints of the legs, including the apex of the tibiae a number of times.

Being a sucking insect, *Phymata* can obviously take food only in liquid or comminuted solid form. Accordingly, the tissues of its prey must be broken down to make them ingestible. That liquification or comminution takes place is evidenced first by the injection of an inflating material,—doubtlessly a liquid, second by the results of the postmortem on the discarded prey and third, the nature of the excreta. Dissection showed the body cavity empty, excepting a small amount of viscid substance which probably consisted of the chitinous indigestible linings of tracheae and intestines. That muscles are reduced during the feeding process was shown also by the semitransparency of the green areas of the exoskeleton after the meal and by the extreme retraction of the abdomen which brought its apex forward in line with the hind edge of the metathorax. The sack-like hind intestine of numerous dissected ambush bugs contained a brown digestive waste. In captivity, this was deposited in the form of a rather dense semifluid which, upon drying, left a sizable residue of solid. This closely resembled fine-grained fudge both in color and texture, and broke into crumby particles when probed. Such deposits were also seen in nature. They seem to prove that *Phymata*, although equipped with piercing sucking organs, ingests finely divided particles of solids with its fluids. The preoral mode of digestion, therefore, is not invariably and solely a process of liquification of solids but may involve also their comminution.

That preoral digestion of muscular tissue is practised by *Phymata* is shown also by observations on other prey than *D.* 12-*punctata*. It was noticed regularly that all prey sucked out by the predator was very easily pierced with an insect pin when mounted, and, moreover, the body seemed lighter and more fragile,—the heads of flies, moths and bees, in particular, breaking off even more readily than usual.

Several miscellaneous observations on other prey species will serve to supplement the above picture of the feeding process. In some cases, comparatively soft-bodied insects, such as Lepidoptera, bees and Diptera, are penetrated through the disks of the sclerites and not always at the sutures and conjunctivae as seems to be done regularly in the instance of hard-shelled beetles. The period of struggle following capture seems to be in proportion to the size of the captive. For example, a moth, *Scepsis fulvicollis*, resisted or convulsed vigorously at intervals during the first 10 minutes following capture, and continued to do so, although with decreasing vigor, for a total of 22 minutes, whereas *Diabrotica* 12-*punctata* and *D. longicornis* seemed to be dead in one to three minutes. The latter have only about one third or fourth the body volume of *Scepsis*. In addition to the reduction of the victim's contents and the resulting fragility of the body, discarded prey,—particularly beetles, may have the wings

extremely disarranged, a condition effected by *Phymata* as it forces itself under the wings in its attempt to pierce the soft dorsum of the gradually shrinking abdomen.

To summarize, the feeding process is characterized by two phases. First, is the preparatory phase, which embraces the injection of a fluid that effects an inflation of the body,—at least that of smaller prey, and probably functions both to kill the captive and to liquefy or comminute its internal tissues. *Phymata pennsylvanica*, and doubtlessly all other members of its family, therefore, possess the type of digestion described as preoral or extraoral. The second phase of the process includes the ingestion of the liquid or finely divided solids. The removal of the contents of the exoskeleton results in an extreme contraction of the telescopic abdominal segments and renders the body parts easily separable because their supporting muscles have been broken down by the digestive agent injected.

Does Phymata Eat Nectar? Two females, one observed on September 14, the other on October 5, were found engaged in introducing their mouth parts deeply into the flowerets of *Helianthus tuberosus* and *Aster multiflorus*, respectively. The insects paused for a few seconds to a half minute each time the feeding organs were inserted, then moved eagerly and more rapidly than usual to the next floret. It may be significant that a brisk wind blew on both days,—a condition found on several occasions to be disadvantageous to preying, presumably because the potential food insects of *Phymata* cling to their supports, or find it hazardous to alight on flowers tossed wildly by the breeze. The hunger possibly resulting from such absence of prey may drive the ambush bug to take nectar as an alternate food substance.

Coupling and Sex vs. Feeding. The term coupling, not synonymous with copulation, is used here to describe that physical relation of a pair of ambush bugs in which the male rests or rides quite inactively on the dorsum of the female. Because the male occupies this position very commonly and sometimes for several consecutive hours, the coupled pair is frequently seen engaged in one phase or another of the feeding process. Numerous observations in the field showed it was the female that caught the prey in by far most of the cases. She usually also held, and fed on, the captives alone, while the male mostly perched passively on her back. Being somewhat smaller and sitting rather far back on her dorsum, the male would seem to be at a disadvantage in the race to seize prey, but he actually does not enter the competition, except rarely. In general, whether thus coupled, or single, the males seem to wait for prey less persistently and to feed less frequently than the females. However, the male occasionally fed on some captives simultaneously with his mate. In one such instance, involving a *Feltia* moth as prey, both took part in holding the victim. In order to participate, the male is obliged to advance from the usual resting place until his head and raptorial legs project beyond the head of the supporting mate. In a few other instances, only the male held and fed on the prey. In general, both when coupled and single, the males caught smaller insects than the larger, more voracious females. For instance, males captured the majority of the fungous gnats reported in Table 1.

Discarding the Prey Remnants. Approximately 10 per cent of the individuals recorded in Table 1 lay dead in flower cups, on the horizontal parts of large leaves, and fastened in the leaf or branch axils of the ambush plants. Without exception, these insects were still soft and flexible when mounted on pins one or more hours after discovery, indicating they had died but recently. Moreover, they invariably lay in flowers still occupied by one or two individuals or couples of *Phymata*, or on leaves and in axils directly below flowers so inhabited. Such discoveries were largely noticed on bright warm days of little or no wind. These conditions favored extensive prey movement and consequent-

ly the capture of comparatively many insects, whose dead, empty bodies sometimes fell upon the plant and remained there until a rising wind shook them free. However, large butterflies, such as *Colias eurytheme*, occasionally hung in the axils on windy days. When a brisk wind is going, fewer insects are caught, and such as are dropped upon plant parts when discarded, obviously fall quite promptly to the ground. The vegetation and soil beneath two isolated ambush plants previously well inhabited by *Phymata* were searched on October 11 and 30. There lay dead Syrphidae, Tachinidae, Calliphoridae, honeybees, butterflies and moths, in short representatives of groups commonly taken from *Phymata* in flowers. Some of these may have died from other causes.

LITERATURE

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A PAPAIPEMA FROM ARIZONA (LEPIDOPTERA).

BY HENRY BIRD,
Rye, New York.

When economic entomology concerns itself in the line of biological control further than the introduction of foreign parasites to offset the inroads of introduced pests and turns for help to our indigenous hordes of balancing agents, as it must do some day, college professors may well direct their students to *Papaipema* biologies. Here an easy exposition of what holds a large genus to innocuous bounds is amply portrayed and, as hosts to such a retinue which goes still further afield, proclaims them in fact helpful species of our biota. Hence additional details, particularly of the food plants selected by this endophytic group presages helpful information. The main aid in securing familiarity with these boring species rests in knowing the larval food preferences, since adults are easily secured through breeding. Such an important feature with an unplaced Arizona form now adds to this knowledge, a heavy composite being chosen. Its larva belongs to that section where the curious coloration pattern in early stages depicts a girdled larva, with longitudinal lines broken at middle, indicative of some ancestral condition where the occupancy of some encircling habitat probably induced the result. Larvae of *P. cerussata* and *rigida* as well as eleven others present this feature. That the genus as a whole exemplifies such pronounced color patterns in early stages, so different from the bulk of mining larvae, aids immensely in their determination, the while it carries implication of phylogenetic and ancestral significance.

This discovery is due to Mr. George P. Engelhardt whose long continued research in the biologies of the Aegeriidae have born such important results. In recognition of this as well as of his many efforts to unravel *Papaipema* matters, it is fitting to dedicate to him

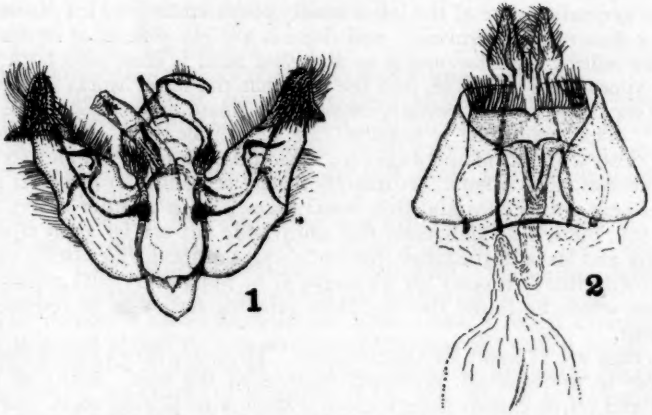
Papaipema engelhardti n. sp.

Adult. Fully congeneric, no marked prominence on frons. Antennae with simple pectinations, no white scales at base. Body vestiture and tuftings heavy, the vertical, anterior thoracic, quadrate tuft most prominent. Ground color even smoky brown with suggestion of faint purplish for the thorax and primaries, the latter with bronzy sheen and over all a scattering of faint white scales. Primaries show little contrast, basal area concolorous and undefined as is the t. a. line; the usual stigmata show only in deeper shading, no indication of white thereon; median shade line of same deeper tone from reniform obliquely inward to hind margin; t. p. line fine, out curved past reniform thence inward to hind margin; subterminal space a shade lighter and vaguely purplish; s. t.

line fine, toothed outwardly on veins; terminal space with vague bronzy sheen, the veins tipped with a faint whitish scale at base of fringes.

The secondaries are of a paler smoky hue, more glistening, the discal lunule and veins slightly defined. Beneath, an even smoky hue rather more glistening and powdered than secondaries.

Expanse 30 mm.; habitat, Oak Creek Canyon, about twenty miles from Flagstaff, Coconino Co., Arizona.



Genitalia of *Papaipema engelhardti* n. sp. 1, male; 2, female.

Larva. Penultimate stage: head rounded, polished, indented slightly at occipital suture, color reddish brown, mouth parts darkened, ocelli black, lacks the dark side line common to *nebris* and others; width 2.8 mm. The dull pinkish tone of the cylindrical body, now less vivid than formerly, appears as an unbroken girdle on first four abdominal segments where the whitish dorsal and subdorsal lines are broken; a considerable area of the thoracic joints whitish as is the body ventrally. The setigerous tubercles are in full complement excepting an absence of IVa on joint ten and show contrastingly in shining black; the leg plates of duller color than the cervical shield which is shining honey yellow, with blackish edging laterally and nearly covering joint one; the crochets are black on the whitish prolegs. Length 25 mm.

Maturity: larva more robust, color has faded to whitish translucence, tubercles the same, I larger on first three abdominal segments than elsewhere, cervical, anal shield and head darker than formerly, the latter 3 mm. in width. Larval length 38 mm.

Pupa. Normal, no frontal angle or development, polished and thin shelled, with short, slender anal spine. Period short, about twenty days.

The following type material is temporarily in collection of author.

Holotype—Male, bred, emerged July 20, 1936. (G. P. Engelhardt) Coconino County, Ariz.

Allotype—Female, same data.

Genitalia—Male and female types on slides.

Larval inflates—Penultimate and last stages, 3 specimens.

Foodplant—Rudbeckia ampla A. Nels.

Remarks. The male genitalia (fig. 1) conforms to the type common to forty congeners. The trigonate, heavily spined cucullus, the strong protruding clasper "curved like a cow's horn" (Smith) arises midway of the harpe bearing

outwardly a few teeth; the aedoeagus with double row of teeth at tip and its single elongated cornuti are the more conspicuous features characterized by Smith when defining the genus. Individuality with *engelhardti* rests in a ridge-like thickening of chitin forming a line which parallels the contour of the harpe, a unique feature, together with minor differences.

The female genitalia (fig. 2), as is general throughout the genus, offers comparative value in the outline and ornamentation of the genital plate. The signum decorates the bursa with a double row of slightly raised nodules.

This species or form is very close to *P. errans* B. & McD., also from Arizona, but a male genitalic figure of the latter kindly prepared by Mr. J. F. Gates Clarke of the type does not conform well, and there is a slight difference in the appearence of the adults. A relationship to *P. nelita* Strk. is close also both in genitalia and appearance of larvae, and the fact that the latter works in *Rudbeckia laciniata*, very close to the western *ampla*, bids pause as to associations in that direction. What might be a parallel case of double food choice and larval similarity exists with *astuta* and *duplicata* in *Collinsonia* however, and *Helianthus* and its followers offers others. Ultimately it may be found a subspecies relationship exists here with *nelita* and this desert form. With another desert denizen, *unimoda* Sm., there is no affiliation; this and *frigida* Sm. are far apart from others on genitalia and larva of the latter, the early stages of the former being unknown.

Mr. Engelhardt reports his discovery to be apparently well represented at two stations where he found the foodplant growing lustily in its required moist environment.

No data are at hand for the parasites. These are sure to hold their usual drastic sway in undisturbed, restricted colonies of the host. Scattered through the larval and pupal careers their inroads assume a surprising total, proclaiming in the end how a single pair will be followed by but a single pair, consumating nature's inexorable law of balance.

NOTES ON THE BIOLOGY OF THE GREAT BASIN TENT CATERPILLAR, *MALACOSOMA FRAGILIS* STRETCH (LEP., LASIOCAMPIDAE)

RALPH B. SWAIN,
University of Colorado, Boulder, Colo.

The great basin tent-caterpillar is the most abundant form of *Malacosoma* found in the Rocky Mountain region of the United States. In Colorado, the species is often a serious pest of the aspen. It feeds upon a wide variety of deciduous trees and shrubs. In the foothills, *Rhus trilobata* and *Prunus melanocarpa* are frequently attacked. Whole aspen groves at higher altitudes are often defoliated by this species. In the mountains, the migrating larvae have occasionally been so numerous as to stop locomotives by greasing the rails with their crushed bodies.

At Boulder, Colorado, where most of these notes were made, *M. disstria*, with which imagoes of *M. fragilis* might easily be confused, also occurs. Larvae reared in the laboratory and used in obtaining the head measurements given below were determined by Dr. W. T. M. Forbes to be those of *M. fragilis* Stretch.

M. fragilis hibernates in the egg stage and has one generation a year in Colorado. The eggs are laid in a single mass on one side of a terminal branch of the host tree. This mass may be roughly circular and about one and a half centimeters in diameter. It is covered by a thick protective layer of a dried frothy substance. The average number of eggs in five egg masses was one hundred forty-three.

Hatching begins in the foothills just as the buds of the choke cherry and skunk sumac are opening. In the spring of 1938, the first larvae were found in the field on April third. They had not yet begun to feed. Egg masses col-

lected the same day and brought into the laboratory hatched within twenty-four hours.

The following data on length of larval stadia and width of head capsule were gathered from observations on a colony reared from a single egg mass collected March 18, 1937, at Boulder Colo., and reared in the laboratory at room temperature.

Larval stadium	I.	II.	III.	IV.	V.	*Pupal plus prepupal per.*
Length in days	4	4	6	6	9	15

Average total period from hatching to emergence was forty-four days.

The greatest width of the head capsule was determined for five larvae in each stadium. The average widths were:

Larval stadium	I.	II.	III.	IV.	V.
Width in mm.	.48	.75	1.28	2.10	3.14

By calculation it is evident that no stadia were overlooked.

In the field a great many more than forty-four days are required for growth from newly-hatched larva to adult. At Ft. Collins, Colo., in 1935, larvae in the fifth stadium were collected June twenty-fourth. From this collection the first cocoon was obtained July fourth; the first moth, July twenty-third; the first eggs, July twenty-ninth.

The web of this tent caterpillar is usually centrally located in the shrub or tree on which the eggs were laid. The first web is often made over or near the egg mass. Later, other webs may be constructed. The bright daylight hours and periods of molting are spent within the protection of the web.

The cocoon is rather thin-walled, white, with a rough exterior. It may measure one and a half to two centimeters in length. Caged larvae preferred to spin their cocoons at the top of the cages. Probably the larvae normally make their cocoons on the trunks or branches of the host tree or neighboring trees.

It would seem that *M. fragilis* should be the logical early season host for many of the parasites that later attack the fall webworm, *Hyphantria cunea* Drury. The latter is the most abundant gregarious caterpillar of the Colorado eastern foothill region. Its larvae are not available to the parasites, however, until mid-June. From a small collection of half-grown larvae of *M. fragilis* in 1935 the writer reared a single specimen of *Rogas* sp. (det. C. F. W. Muesebeck), a primary parasite, and numerous adults of the genus *Tetrastichus* (det. A. B. Gahan). The latter issued from cocoons probably made by *Rogas*.

NOTES ON SYMPISTIS KOLTHOFFI AURIV. AND SYMPISTIS ZETTERSTEDTI LABRADORIS STAUD. FROM CHURCHILL, MANITOBA (LEPID. PHALAENIDAE) *

BY T. N. FREEMAN,
Ottawa, Ont.

Sympistis kolthoffi Auriv. was originally described from Greenland (1890, *Anarta kolthoffi* Aurivillius, Bihand Till. K. Sv. Vet.-Akad. Handl., XV, 20, pl. 2, fig. 1) as a race of the European *S. zetterstedti* Staud., and has not been previously recorded from North America. Specimens of *kolthoffi* from Churchill, Manitoba, agree very favorably with the original description and figure, and appear specifically distinct from specimens of *labradoris* from the same and other Canadian localities.

Judging from a limited number of both species taken at Churchill by W. J. Brown in 1937, it would appear that *kolthoffi* flies earlier than *labradoris*, the former from June eighth to the thirtieth, and the latter from July eigth to the fifteenth. Other Churchill specimens of *kolthoffi* collected by A. T. Harper in 1933 range from July first to the sixteenth, much later than in 1937, but unfortunately I have no specimens of *labradoris* of the same year for comparison.

*Contribution from the Division of Entomology (Systematic Entomology) Department of Agriculture, Ottawa.

The male genitalia in several specimens of each species have been examined but apparently lack constant structural characters by which they may be separated. However, it is believed that *kolthoffi* and *labradoris* are specifically distinct and not merely geographical races, since both occur at Churchill and show no tendency toward intergradation of wing pattern. In the primaries of *kolthoffi* the light grey basal and terminal areas contrast with the much darker median region and consequently the maculation appears much more distinct than that of the dark almost unicolorous *labradoris*. In addition to this difference, *kolthoffi* possesses a distinct ferruginous collar which is hardly noticeable in the other species.

A NEW SPECIES OF DICTYA (SCIOMYZIDAE, DIPTERA).

BY GEORGE STEYSKAL,

Detroit, Michigan.

Dictya currani n. sp.

Male. Wings with two brown spots in apical portion of subcostal cell. A row of about six short stout bristles on the distal half of the posteroventral surface of mid femora. Prosternum with a few hairs anteriorly and posteriorly, and a few hairs also present on the middle of the propleura in front of the spiracle. Genitalia similar to *D. pictipes* Loew, except the anterior claspers (see figure), which are bent forward hookwise, narrowly laterally expanded at the apex, and with a thin transparent web in the sinus of the hook.

Dictya currani n. sp.

Female. Similar to the male except the genitalia. The eigth abdominal sternite is very similar to Curran's figure of *D. borealis* (1932, Amer. Mus. Novitates No. 517, p. 5, fig. 13).

Length of both sexes, 3.5—5 mm.

Holotype, male, Thunder River, Quebec, Canada, June 19, 1930 (W. J. Brown) and *Allotype,* female, Isle Royale, Michigan, August 3-7, 1936 (C. Sabrosky), in the American Museum of Natural History. *Paratypes,* four males and two females, same data as allotype, in the collections of Mr. C. W. Sabrosky and the author.

This species is the only known species besides the one identified by Curran, Malloch and the author as *Dictya umbrarum* Linnaeus which has hairs on the prosternum and in the middle of the propleura. The author takes pleasure in dedicating this species to Dr. C. H. Curran.

BOOK REVIEWS

Atlas of the Scale Insects of North America. Series II. By G. F. Ferris, Stanford University Press, Stanford, California. 132 pieces. Looseleaf form $7.75; bound $8.75.

As stated in the first series of this work published in January, 1937, the Atlas is an attempt to make possible the identification of the scale insects of North America, from the Arctic Region to the Panama Canal Zone. Although based on a number of important collections of scale insects made during the past forty years, the author intends to include any new species which may come to hand during the course of the work. In order to facilitate the classification of new species and the species already known, the family Coccidae has been raised to superfamily rank—superfamily Coccoidea—and eleven families have been proposed for the North American species.

The Atlas has been prepared for use in looseleaf form, or as a bound volume. The species are uniformly treated each in a four-page folder with the text matter opposite a full page of figures and preceded by a title page. Since each species is complete in a flolder, any species or group of species may be obtained separately. The most important genera are similarly treated, with a page of morphological figures opposite the text. With each species the page of figures usually includes the antennae and cephalic margin of the first stage; habit; antennae of adult female; anterior spiracle of adult female; pygidium of adult female; and dorsal and ventral aspects of detail of adult female pygidial margin. As separate folders the arrangement of the Atlas is admirable, but as a bound volume it is rather bulky, due to the repetition of title and blank pages. The latter, however, might be used for supplemental notes.

Series I and II both deal with the family Diaspididae, subfamily Diaspidinae. Series I contains thirty-four genera of the tribe Diaspidini. Series II contains seven more genera of the Diaspidini, four genera of the Odonaspidini, one genus of the Xanthopthalmini, and twenty-two genera of the Aspidiotini.

This work presents these scale insects in a comprehensive manner, greatly facilitating their identification. It should prove its usefulness to those interested in these insects, wherever they may reside. When completed, it will be a work of unusual thoroughness and merit.

History of American Beekeeping. By Frank C. Pellett, Editor of the American Bee Journal, Collegiate Press, Inc., Ames, Iowa. 213 pages, 97 illustrations. $2.50.

In this short account of American beekeeping, the author has dealt almost entirely with the period from the earliest American records up to 1914-18 when conditions contingent on the World War changed beekeeping from the status of a hobby to that of an industry. With this change in the nature of beekeeping, the 'honey producer' replaced the old-time 'naturalist' beekeeper, and leadership in the field passed from the 'men living with the bees' to trained men in federal or state institutions.

In this small volume the author has manged to give a fairly complete account of the diverse aspects of American beekeeping—without becoming encyclopaedic or losing sight of the 'human factors'. The twenty-five short chapters indicate the scope of the volume.

I. Beginning of American Beekeeping. II. Langstroth's Invention of the Bee Space. III. The Comb Honey Era. IV. The Hive Controversy. V. Introduction of the Waxmoth. VI. Smokers, Excluders, Etc. VII. Wax Foundation and Reinforced Combs. VIII. Importation of New Races of Bees. IX. Invention of the Honey Extractor. X. Bees in California. XI. Rise of Commercial Queen Raising. XII. Search for Controlled Mating. XIII. Migratory Beekeeping. XIV. Beekeepers' Societies and the Convention Period. XV. The *American Bee Journal.* XVI. *Gleanings in Bee Culture.* XVII. Other American Bee Periodicals. XVIII. American Books on Bees. XIX. Pioneer Commercial Honey Producers. XX. The Trade in Live Bees. XXI. Improving Bee Pasture. XXII. Sweet Clover and Specialization. XXIII. Efforts Toward Disease Control. XXIV. Beekeeping Memorials. XXV. Adulteration of Honey and Pure Food Legislation.

R. H. Ozburn.

EXCHANGES

NOTICE—The regulations under Destructive Insect and Pest Act require a permit to import living insects into Canada. Applications for permits should be addressed to the Secretary, Destructive Insect and Pest Act Advisory Board, Department of Agriculture, Ottawa.

STAPHLYINIDAE—Unidentified or identified, wanted in exchange for identified Coleoptera from Southern Calif. Esp. Bledius, Stenus, Philonthus, and Staphylinus. A. Watson, San Diego Nat. Hist. Museum, Balboa Park, California.

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WANTED—Megathymus streckeri from S. W. Colo. or New Mex. Also from Texas. Also M. yuccae from Colo. Offer in exch. Meg. leussleri Holl. (Nebr. race streckeri) R. A. Leussler 115 S. 52 St. Omaha, Nebr.

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